

FLORAL ANATOMY OF *RHEXIA VIRGINICA* (MELASTOMATACEAE)

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Contradictory comments concerning the flowers of *Rhexia* L. are found in the two current manuals of our northeastern flora. The description in Gray's Manual (Fernald, 1950) clearly implies an inferior or partially inferior ovary: "Hypanthium urceolate, adherent to the ovary below and continued above it." In contrast, Gleason and Cronquist (1963) report "hypanthium free from the ovary." From serial sections of flowers we have learned that this point of confusion is caused by a developmental peculiarity; viz., cell layers in the fruit wall separate prior to dehiscence in such a way that the partially inferior ovary can appear superior. Flowers of *Rhexia* have unilocular anthers, another unusual feature; therefore we have thought it worthwhile to describe in some detail the reproductive structures of one species, *R. virginica* L.

This investigation originated from conversations between the first author and Dr. John J. Wurdack, a specialist in the taxonomy of Melastomataceae at the Smithsonian Institution, and was carried out during the summer of 1966 while the second author was supported by the Smithsonian Institution's Summer Program for Students. Dr. Wurdack assisted by supplying specimens and information and by reading our manuscript critically.

Flowers, flower buds, and developing fruits were obtained from plants of *Rhexia virginica* var. *virginica* cultivated in the garden of Dr. and Mrs. J. J. Wurdack in Beltsville, Maryland, these plants having been obtained originally from natural stands in the vicinity. A voucher specimen (*Wurdack 2534*) has been deposited in the U.S. National Herbarium.

Serial sections 10-15 μ thick were prepared with a rotary microtome, after fixing in formalin-acetic acid-ethanol, dehydrating in a t-butanol series, and embedding in "Paraplast." The sections were stained with tannic acid, ferric chloride, safranin, and fast green. Altogether, more than 50 flowers and developing fruits were prepared in this manner. For 3-dimensional examination of the vascular pattern, we cleared about 20 flowers, utilizing both the chloral-lactophenol method of Amann (Bersier & Bocquet, 1960) and the simultaneous clearing and staining method of Fuchs (1963). Fuchs' procedure, involving prolonged immersion of the material in 10-15% NaOH, had to be modified somewhat, for concentrations of this strength tend to macerate the softer floral tissues. We found that a 5% solution of NaOH could be used, thus reducing the maceration to within tolerable limits. Cleared flowers were dehydrated with an ethanol series and transferred to toluol for examination, thereby hardening the tissues enough to permit manipulation with camel's-hair brushes.

Line drawings were prepared by the second author with the aid of a Wild M5 Stereomicroscope and drawing attachment. Photographs are by Jack Scott, Smithsonian photographer.

Rhexia virginica is an erect perennial herb (often somewhat woody), widely distributed in eastern North America. The flowers, produced throughout the summer in open cymes, are conspicuous for their four showy purple petals and bright yellow stamens. These are borne near the summit of an urceolate hypanthium, which terminates in four short calyx lobes, the lower part of the hypanthium being partially adnate to a four-locular inferior ovary. The locules are in the same radii as the petals — as Eichler (1878) emphasized, this is an exception for the family — and each contains a massive axillary placenta with many bitegminous ovules. The tabular upper part of the hypanthium surrounds an elongate style with truncate stigma. Before anthesis the petals, like those of other Melastomataceae, are tightly overlapped in the configuration known as "right con-

tort," or "right convolute," to use Eichler's (1878, p. 480) term.¹

Prominent multicellular trichomes with globose glandular heads occur on the exposed abaxial surfaces of petals, on the exterior of the hypanthium, and on the superior part of the ovary. Although Holm (1907) found trichomes of two kinds on the leaves and stems of *Rhexia virginica*, all of the floral trichomes are alike. They resemble Holm's Fig. 6, except that the glandular heads are not papillose. Elsewhere in the Melastomataceae, a family noted for the great diversity of its trichomes, the *Rhexia* type has been figured from at least three genera, *Dissotis* (Feissly, 1964, Fig. 13), *Comolia* (Pflaum, 1897, Fig. 17) and *Sonerila* (Palézieux, 1899, Fig. 13B). Feissly's drawings convey quite accurately the dense cytoplasm of the head. This terminal structure does not usually persist through microtechnical procedures; almost all of the trichomes in our sections were "decapitated."

Before the flower opens, the stamens are bent inward in the manner characteristic for the family (Fig. 1), with their apices inserted in eight pockets around the upper part of the ovary. Ziegler's (1925) illustrations show that the pockets ("Gruben") in Melastomataceae with dimorphic stamens are of two depths, those ensheathing the long antesepalous stamens being much deeper than those ensheathing the antepetalous stamens. Adjacent pockets in *Rhexia* differ slightly in depth, even though all stamens are superficially alike, and cross sections through the tips of the incurved anthers indicate that the antesepalous stamens are actually a bit longer than their neighbors (Fig. 14).

¹In order to appreciate the right-handedness of the configuration, it is necessary to imagine a "bug's-eye" view from inside the corolla or to hold up page 7 of Eichler's *Blüthendiagramme* and view his Fig. 1E through the opposite side by transmitted light. The normal botanist's-eye view of a flower bud, from above and outside the corolla, shows each petal overlapping its neighbor to the left. Readers who are interested in the history of this rather puzzling convention should consult Appendix C of B. Daydon Jackson's "A Glossary of Botanic Terms." (For additional confusion, see also Schoute, 1935, p. 25.)

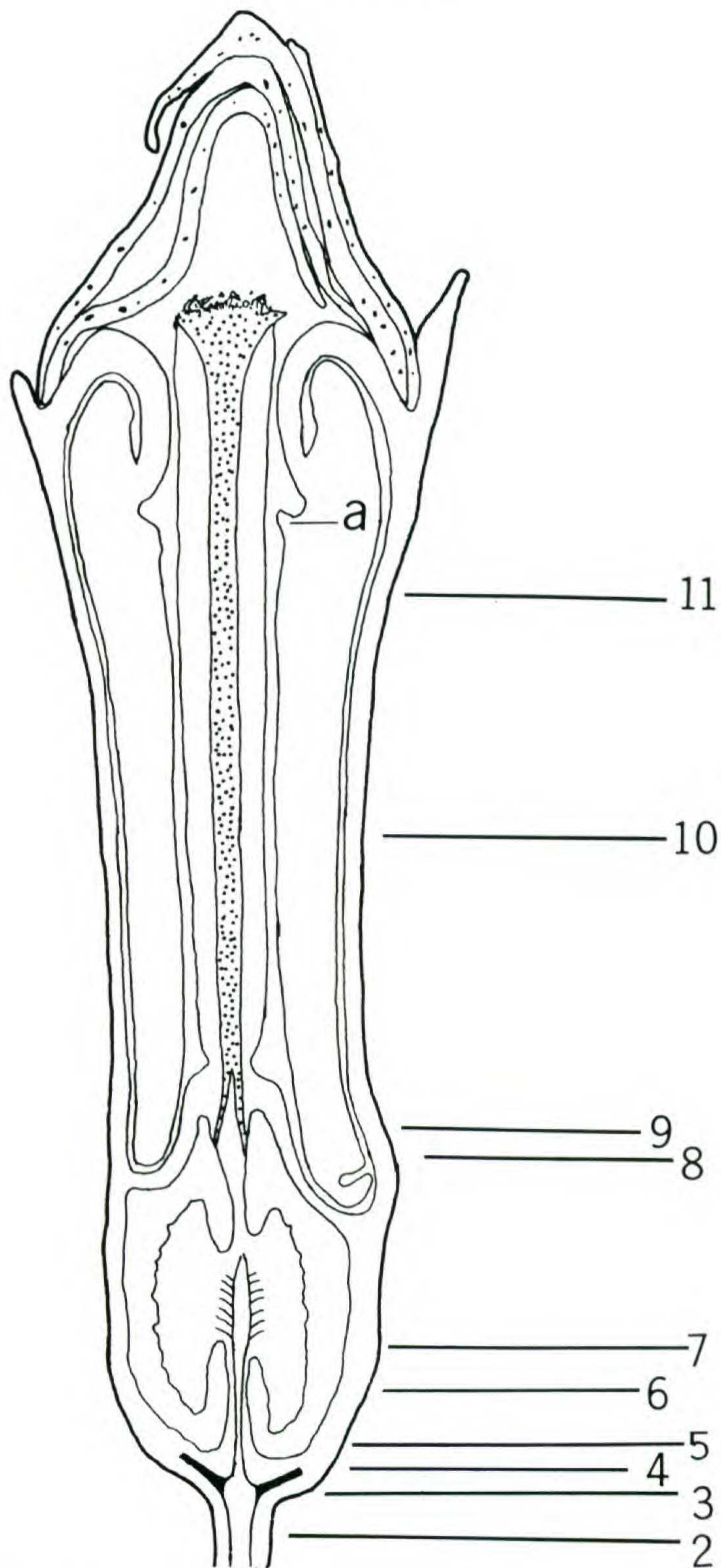
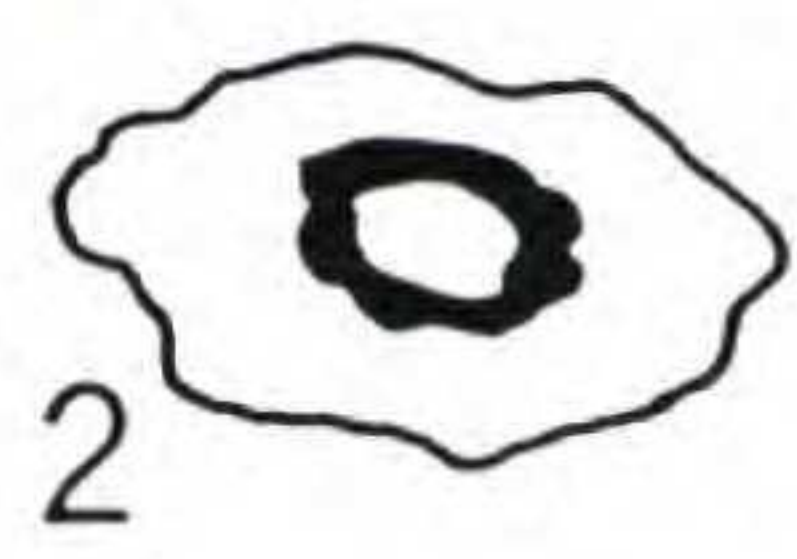
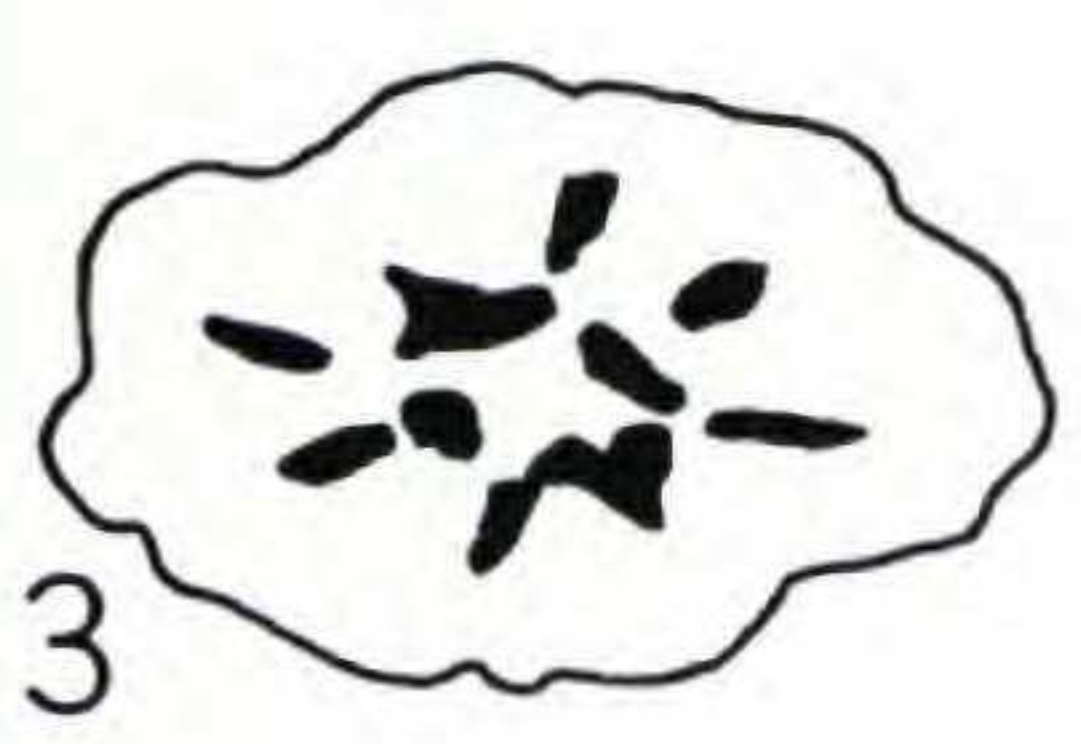
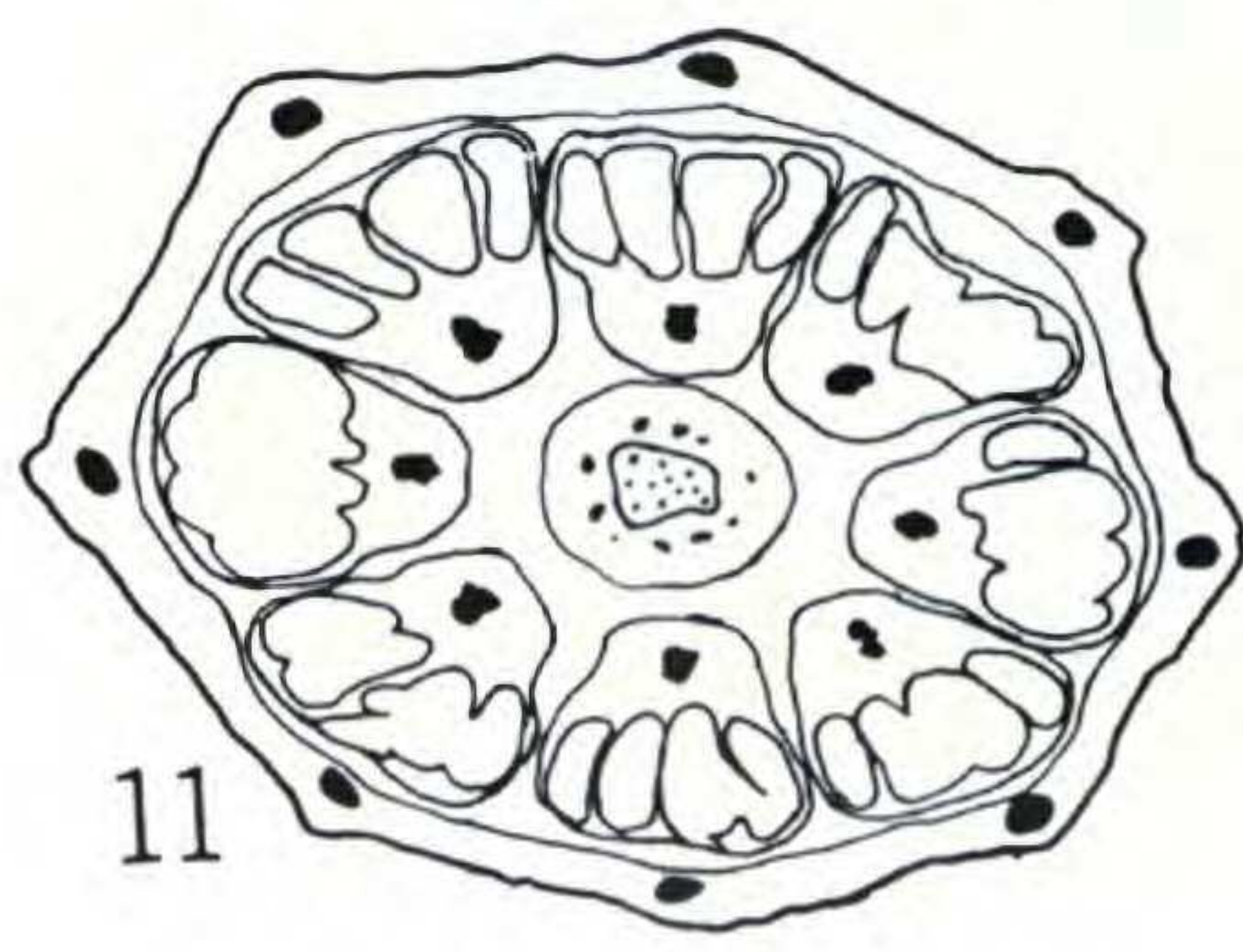
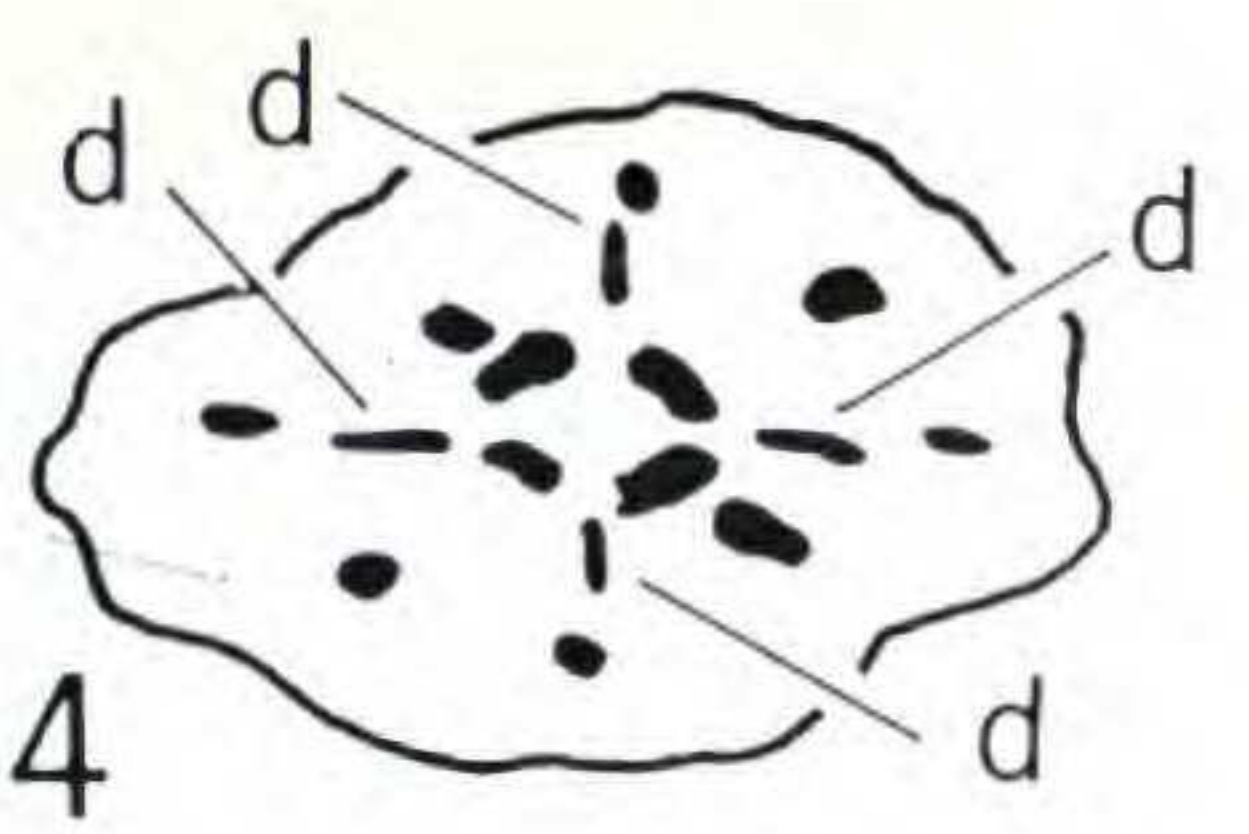
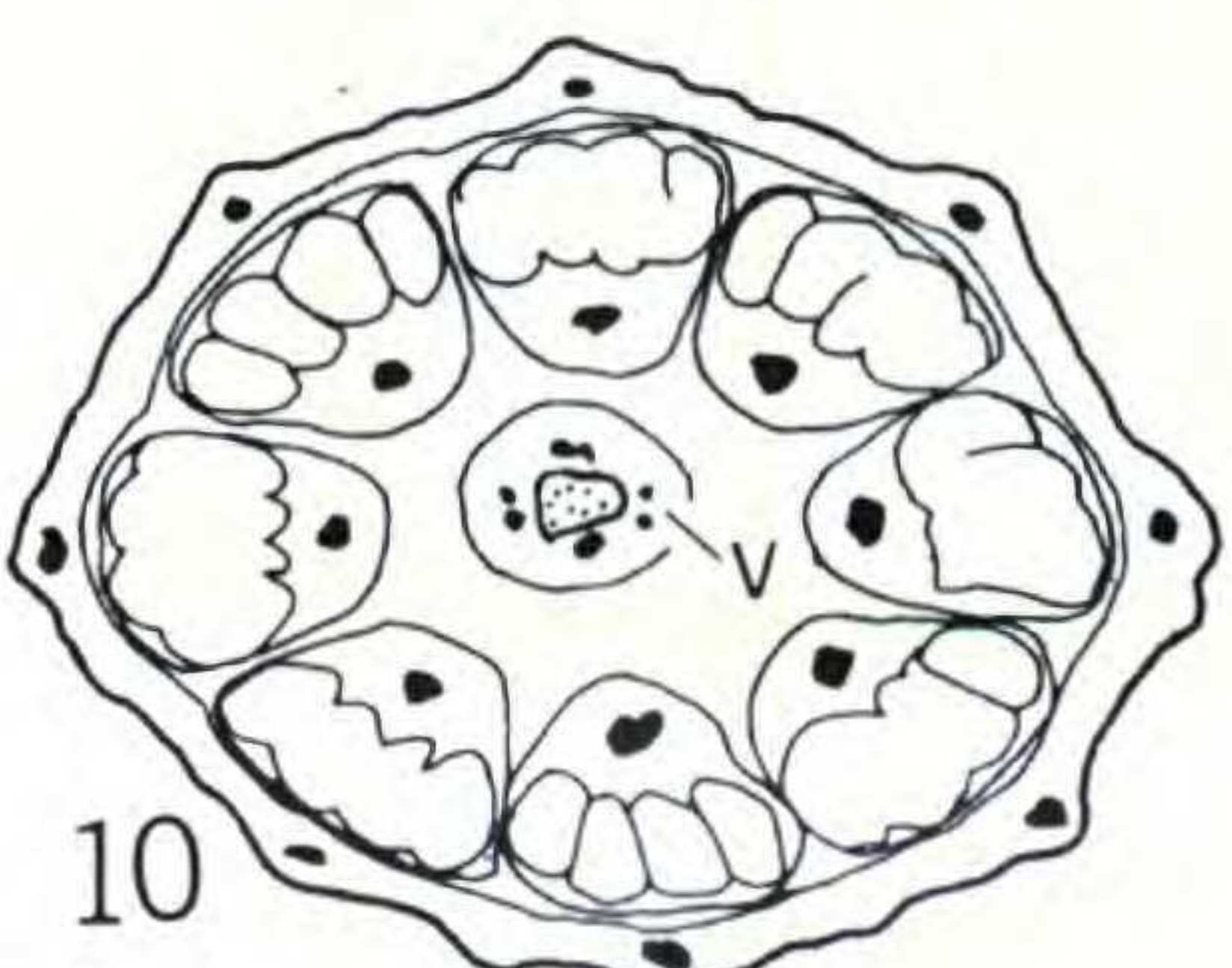
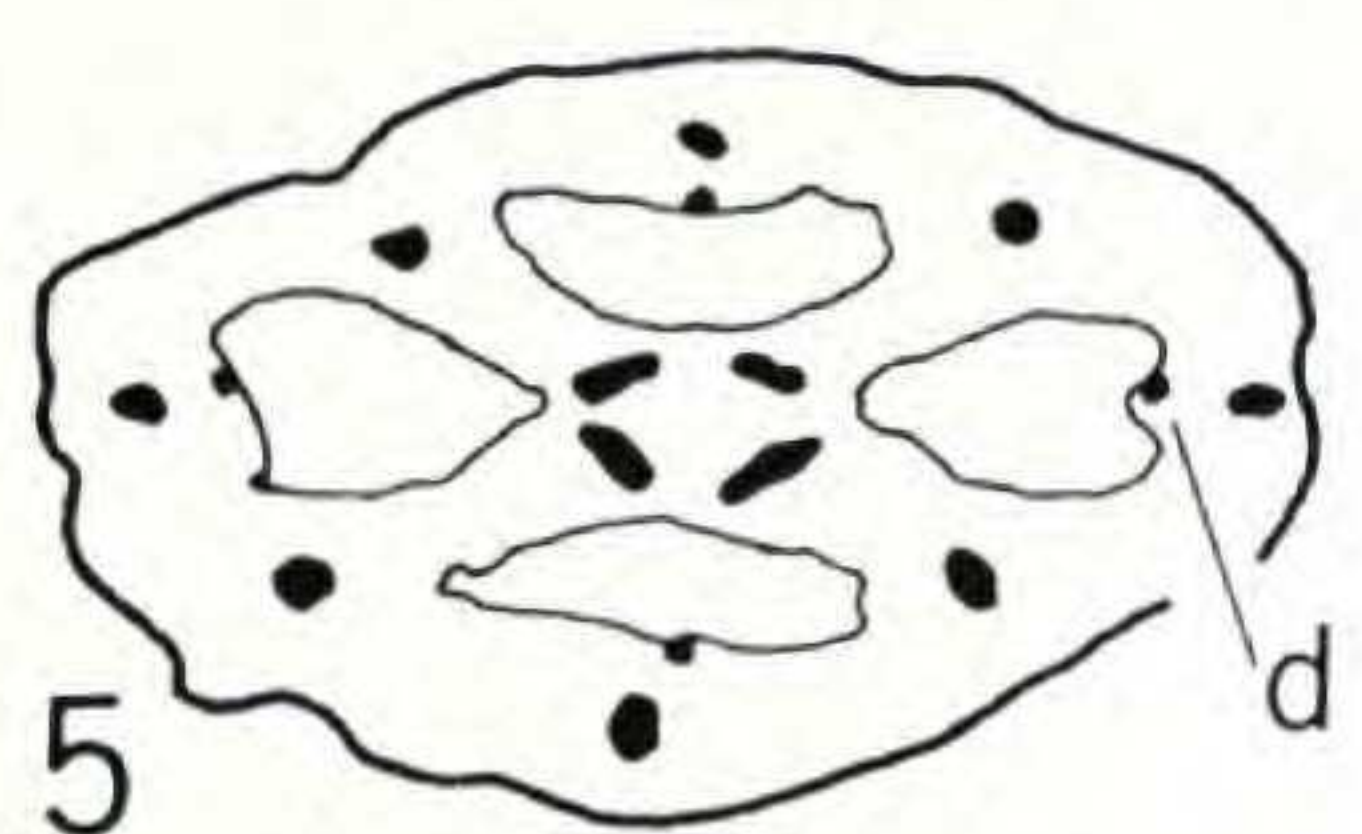
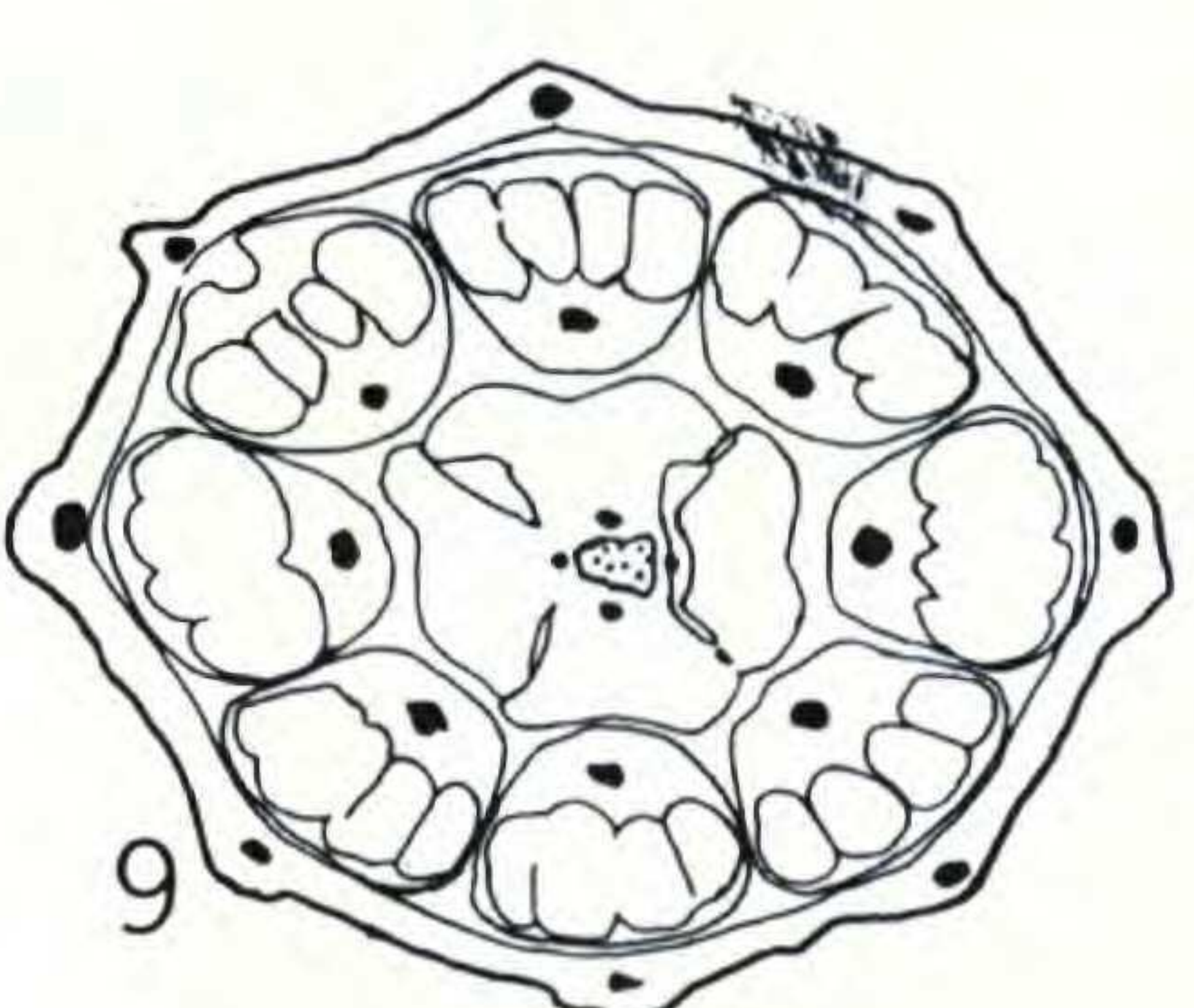
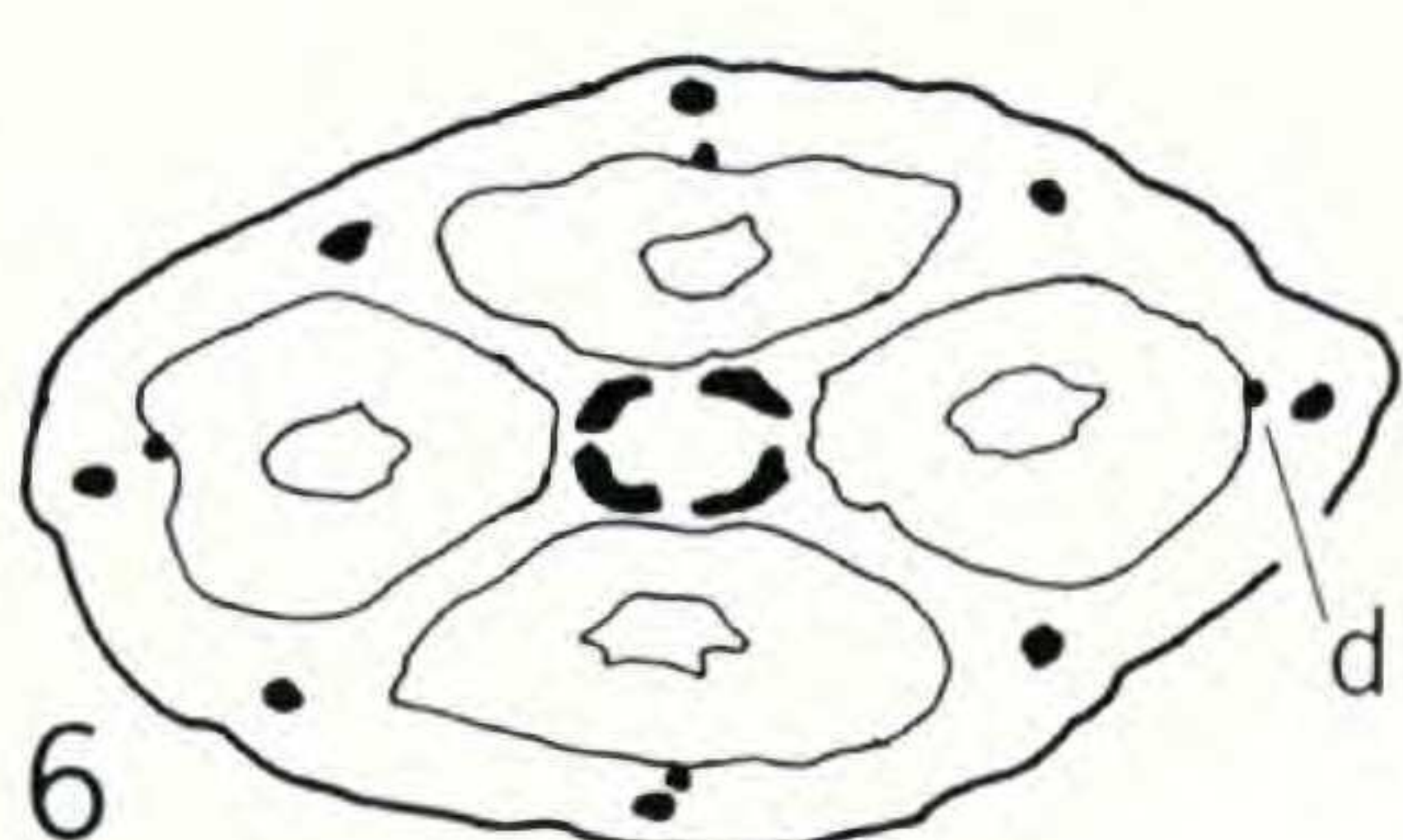
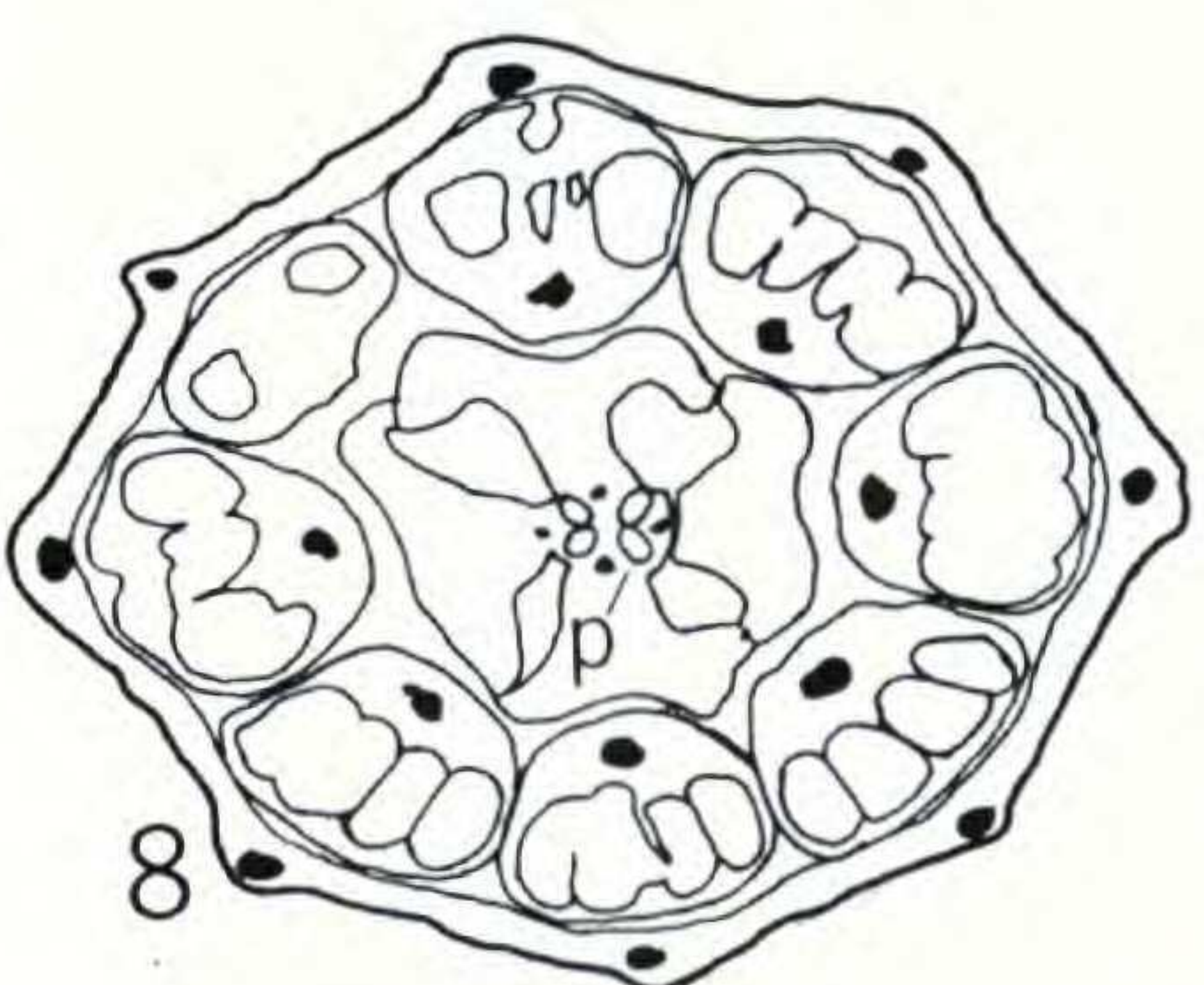
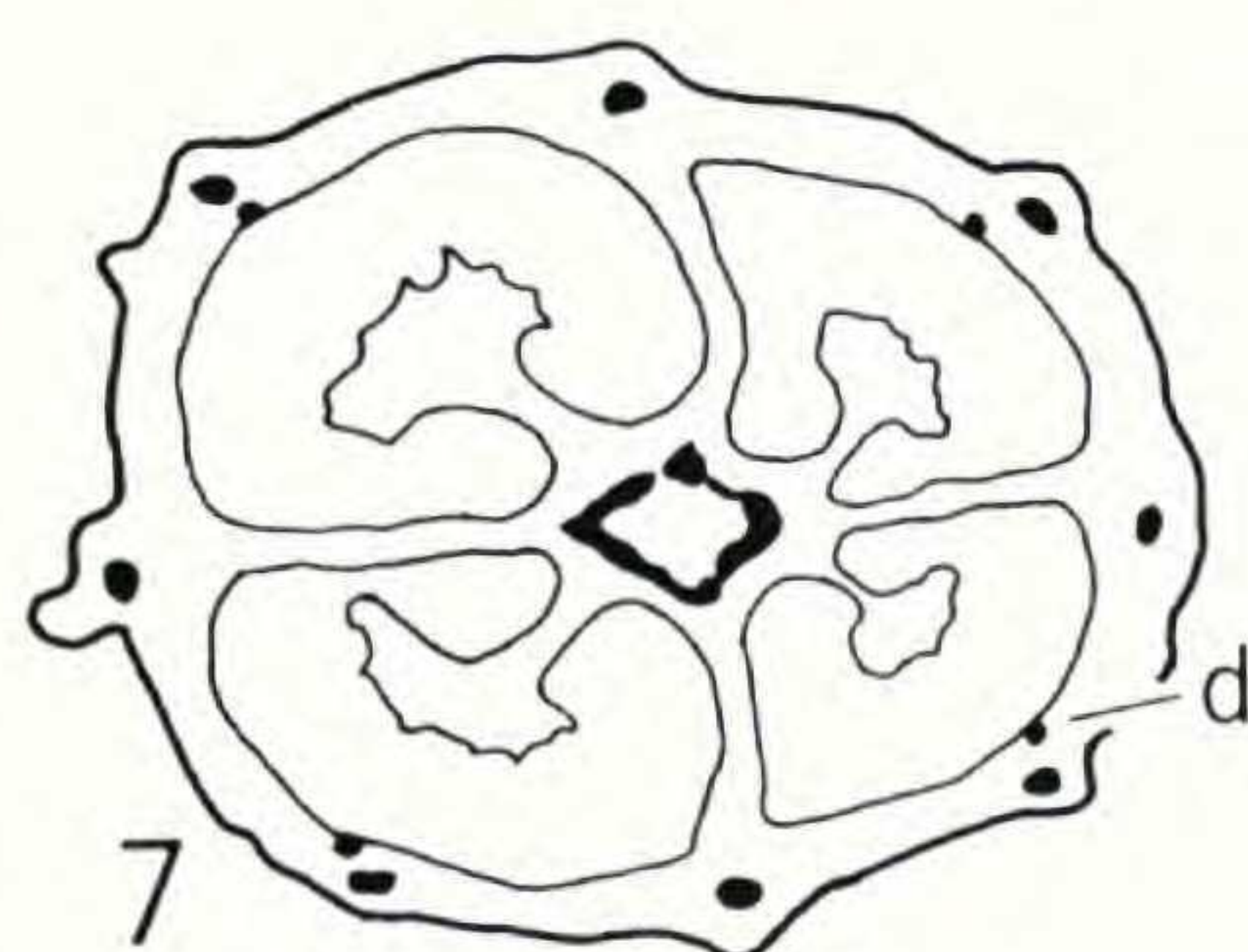


Fig. 1. Flower of *Rhexia virginica* before anthesis; diagram of longitudinal section. Numerals indicate levels of the sections in Fig. (Legend continued to foot of page 169)



VASCULAR SYSTEM

Melastomataceae is one of several families with internal phloem. This character can be observed in some of the floral vascular bundles of *Rhexia* when they are completely differentiated, but the position of phloem elements is somewhat variable and difficult to establish in many cross sections; therefore we have illustrated the vascular system in Fig. 1-11 without indicating xylem and phloem.

Major features of vasculature in the *Rhexia* flower can best be understood by following cross sections from base to apex, beginning with the vascular cylinder of the peduncle (Fig. 2). The lowermost vascular strands to separate from this cylinder are eight large bundles that pass through the hypanthium to perianth members and stamens. Our Fig. 3 shows six of the eight separating a bit lower than the other two (which in this case lead to two calyx lobes). We have found this "six-and-two" pattern to be common, but it seems to have no special significance. The next bundles to separate from the central cylinder are the four dorsal carpellary bundles (indicated by the letter d in Fig. 4-7). The dorsals consist of only a few cells in cross section and are therefore easily overlooked. They originate just below the locules and remain immediately adjacent to the locules throughout their length, ultimately ending in the "roof" of the ovary, below the styles.

It can be seen in cleared preparations that the central axis of the flower contains an anastomosing complex of longitudinal bundles from which numerous transverse placental bundles branch in ladder-like fashion (Fig. 1). The complex originates from the basal vascular cylinder, and represents the combined ventral bundles of the four carpels; however, individual ventrals are not clearly distinguishable below the stylar level. Instead, many cross sections show an almost complete vascular cylinder in the axis (Fig. 7); others show four patches of vascular tissue in a more or less square arrangement (Fig. 5, 6). In successively higher sections taken above the placentae, the amount of central vascular tissue decreases until only four slender strands

remain in the superior part of the ovary, where they alternate with the four pollen transmitting tracts. (We have not attempted to show the distal continuation of the central vascular system in Fig. 1, but see Fig. 8-11). In the style the tracts merge in a broad column of transmitting tissue and each of the vascular strands divides, yielding four pairs of ventral carpellary bundles (Fig. 10) that branch irregularly below the stigma, forming an irregular ring in cross section (Fig. 11).

Four of the eight hypanthial bundles pass into the calyx lobes as midveins. The other four divide at the perianth level into three strands, a central strand supplying a petal and two lateral strands passing into the adjoining calyx lobes. In addition, each hypanthial strand provides a bundle to a stamen, this separation also occurring at the perianth level. All of these longitudinal bundles are united in the upper part of the hypanthium by a continuous transverse vascular complex that underlies the torus.

In common with many genera of Melastomataceae, *Rhexia* has a prominent appendage (Fig. 1) on the abaxial side of each stamen, vascularized exactly as Wilson (1950, Fig. 14) portrayed it. Wilson's interpretation that the vascularized appendages are vestiges of primitive telomes has not convinced other botanists (Eames, 1961, p. 133, 134; James, 1956, p. 209, 210; Leinfellner, 1958).

Floral vasculature of *Rhexia* resembles closely that of *Aciotis fragilis*, which Morley (1953, p. 264 and Fig. 44) chose as an example of a relatively unmodified member of the family. A difference worth noting, however, is that the

2-11. In many flowers, the dorsal appendage (a) of the anther is longer than the example shown here. Trichomes have been omitted from this and succeeding drawings.

Fig. 2-11. Cross sections of an unopened flower (cf. Fig. 1). Some of the diagrams include features from more than one section, and Fig. 7-11 are oriented somewhat differently from Fig. 2-6. All dorsal carpellary bundles (d) are labeled in Fig. 4, only one of the four in Fig. 5-7. p = pollen transmitting tissue (Fig. 8; stippled in Fig. 9-11); v = ventral carpellary bundles. Further explanation in text.

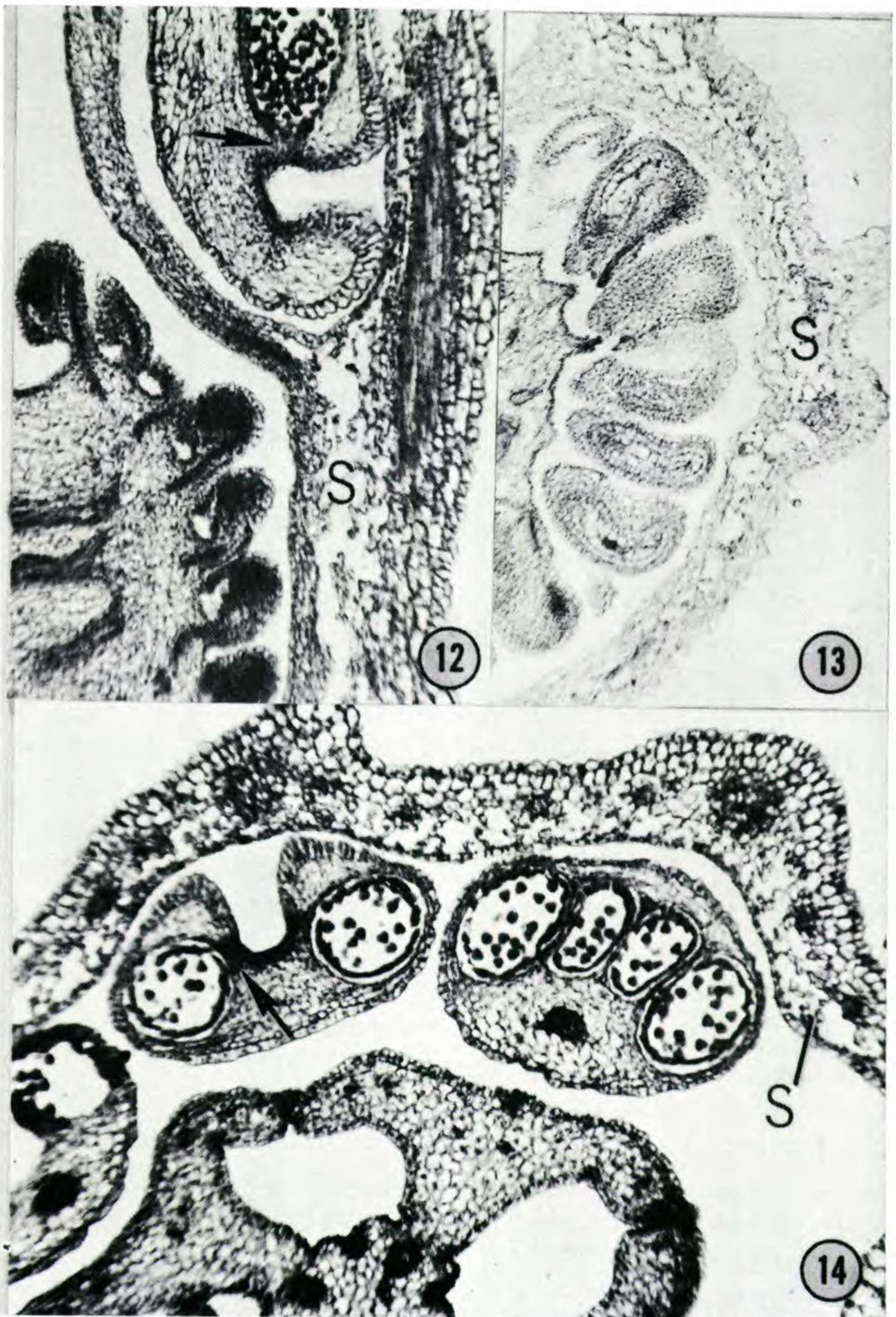


Fig. 12-14. Flowers of *Rhexia virginica* before anthesis, showing aerenchyma (s) of ovary wall and hypanthium. Arrows on anthers indicate "Öffnungsgewebe" of Ziegler (see text).— Fig. 12. l.s., $\times 85$. — Fig. 13. x.s. through inferior part of ovary, $\times 60$. — Fig. 14. x.s. through hypanthium and anthers. Section passes through pore in antipetalous anther, but pores of adjoining anthers are below plane of section; this suggests a slight dimorphy in length of stamens, $\times 90$.

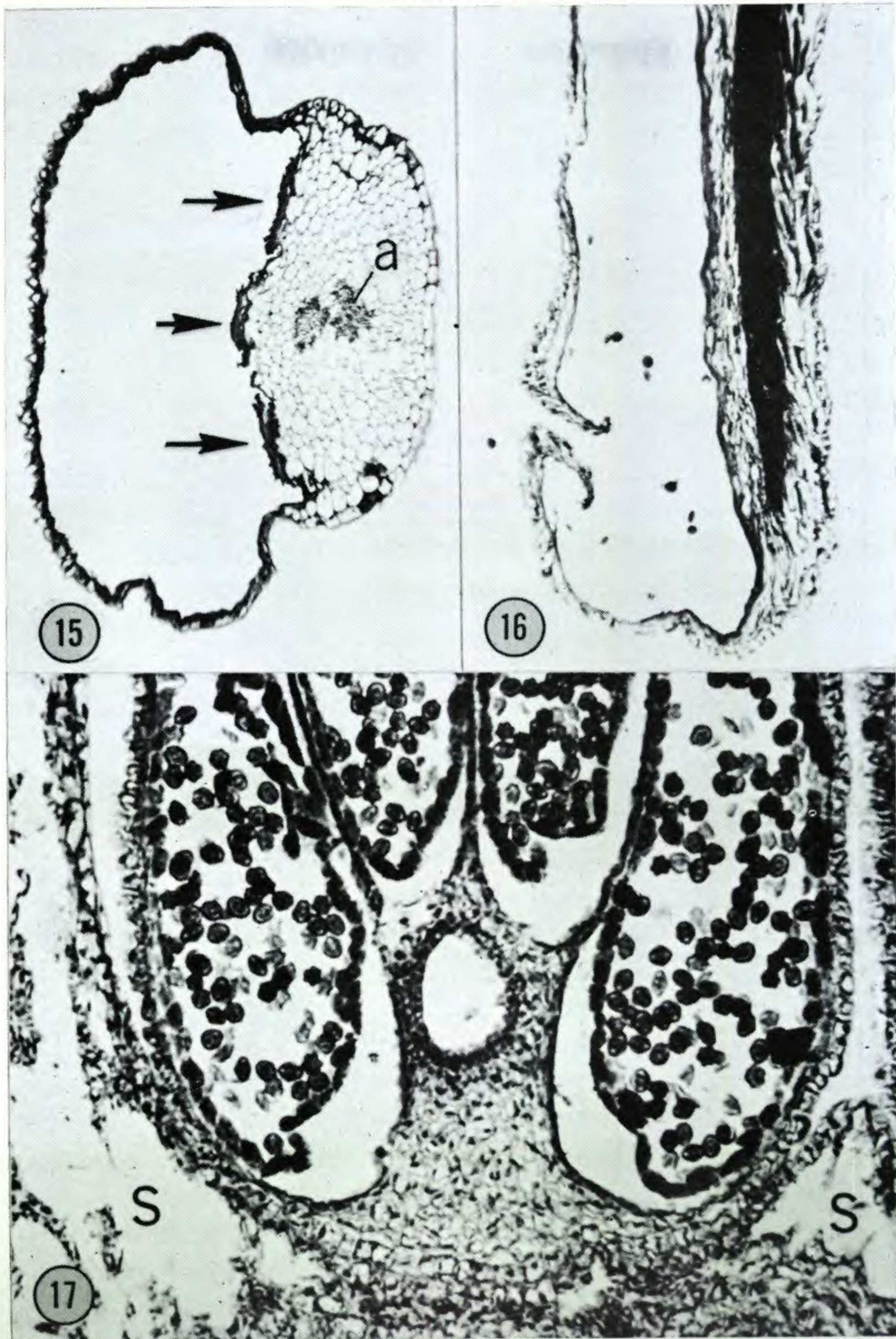


Fig. 15-17. Stamens of *Rhexia virginica*. — Fig. 15. Empty anther, x.s. showing crushed remnants of septa (arrows); vascular tissue on right (a) supplies dorsal appendage, $\times 70$. — Fig. 16. Tip of anther, median l.s. showing pore, a few remaining pollen grains, $\times 55$. — Fig. 17. Tip of anther before anthesis, l.s. roughly paradermal to hypanthium, showing pore (center) and four sporangia. Separation of aerenchyma tissue (s) has been exaggerated in the preparation of sections, $\times 220$.

dorsal carpellary bundles in *Aciotis*, and in other genera that Morley figures, extend into the styles; whereas in *Rhexia* the dorsals terminate at the stylar base, and the ventral complex supplies the style.

HISTOLOGY OF OVARY WALL

In its basal, inferior portion, where carpellary tissues merge indistinguishably with hypanthial tissue, the compound ovary wall of an immature flower comprises 8-12 cell layers. The free portion is thinner, about six cell layers in most places. It is thinnest along the midline of each carpel (Fig. 8, 9, 14), where the cells do not enlarge appreciably during growth, a phenomenon related to the presence of the poorly differentiated dorsal bundle. Dehiscence of the mature fruit begins along these dorsal midlines, and is thus loculicidal.

During development, druses become abundant in cells of the gynoecium, as elsewhere in the flower. Other types of crystals, tannin cells, and isolated sclereids are absent.

Cells of the very young ovary wall are rectangular in outline when examined in transverse or longitudinal sections, and the epidermal layers retain this appearance as the flower develops (except where papillae and multicellular trichomes develop on the outer epidermis). Cells of the layer subjacent to the outer epidermis also remain rectangular in outline. In the inferior part of the ovary, however, the deeper cell layers develop intercellular spaces (Fig. 12, 13). The result is a tissue much resembling the spongy mesophyll of leaves, the individual cells being very irregular in form. Similar developmental changes take place in the free portion of the hypanthium (Fig. 14), but not in the superior part of the ovary wall. The aerenchymatous zone is one of irregular cell contact, where separation occurs quite easily during the preparation of sections (see especially Fig. 17). In the same manner, tissues in the inferior part of the ovary can separate — beginning in the radii between the staminal pockets — when flowers and fruits dry under natural conditions or in a plant press. To an observer aided only by hand

lens and razor, the ovary may then appear completely superior.

ANTHER

Unilocular anthers are known to occur in several plant families, but the unilocular condition is brought about in most cases by the ontogenetic union of two locules (Maheshwari, 1950, p. 39). The condition found in *Rhexia* — four locules uniting at maturity to form one — is rare.² As in some other Melastomataceae (cf. *Centradenia*, *Heeria*; Ziegler, 1925), sporangia develop in a parallel arrangement. *Rhexia* is believed to be the only genus of the family, however, in which all three septa regularly deteriorate before anthesis (see James, 1956, p. 204, for comments on this point by Asa Gray and contemporaries). At early stages of development each septum is made up of three or more cell layers, but the cells gradually disintegrate through the activity of the uninucleate tapeta. Eventually the tapetum of one sporangium is juxtaposed to that of the neighboring sporangium with only fragments of cell walls between them. Rupture of these tenuous partitions occurs more or less simultaneously throughout the length of the anther (Fig. 8-11), and the central septum persists no longer than the others. The breaks occur toward the adaxial side, so that cross sections prepared after pollen has escaped show the flattened remnants of septa on the connective side (Fig. 15).

At the time of dehiscence, the anther wall comprises two cell layers, neither of which has the irregular banded wall thickenings of the "endothecium" or "fibrous layer"³ in a typical textbook anther. Some local modification of the epi-

²Eames (1961, p. 114) gives as examples *Arisaema*, *Callitriche*, *Clusia*, but cites no references. We have come across published comments on anther development only for *Callitriche*. Anthers of the latter have a very different form from those of *Rhexia*, and unilocularity develops only near the apex; the lower part of the anther is bilocular at maturity (Hegelmaier, 1864, p. 39).

³See Eames (1961, p. 125, 138) for a discussion of these terms. Some Melastomataceae do have a fibrous layer. In lacking a fibrous layer, *Rhexia* resembles *Melastoma malabathricum* and *Mouriri guianensis*. (Subramanyam, 1948; Venkatesh, 1955).

dermal cells takes place during development, those at the base of the anther becoming papillose, and those surrounding the pore becoming transversely elongate (Fig. 12, 14, 16), but overall thickening of the cell walls is negligible.

Pollen emerges through a solitary pore located near the apex of the anther on its adaxial side. The pore is circular to elliptical in sectional outline (Fig. 17) and only about .05 mm in diameter.⁴ It originates as a distinct depression early in the development of the anther. About five layers of cells surrounding the interior of the pore and separating it from the sporogenous tissue remain small and stain densely throughout the development of the anther (Fig. 12, 14). Ziegler (1925) used the term "Öffnungsgewebe" to describe an identical tissue in *Centradenia*, the anthers of which are histologically similar to those of *Rhexia*. The small size and dense appearance of the cells invite comparison with the "resorption tissue" by which anthers of certain Ericaceae dehisce. To judge from publications on Ericaceae, however, cells surrounding the *Rhexia* pore differ in two ways: (1) they lack the calcium oxalate crystals of ericaceous resorption tissue (Matthews & Knox, 1926), and (2) they do not "become converted into an amorphous, apparently fluid mass" (Copeland, 1943).

In most families with poricidal anthers, a derivation from septicidal dehiscence is evident upon inspection, for the pores are in pairs, are somewhat elongate along the lateral furrows, and open with the aid of a fibrous layer (Leclerc du Sablon, 1885). Complete transitions can be shown in some plant groups from anthers opening longitudinally to anthers opening apically (see, for instance, Venkatesh, 1957). A similar progression has been proposed for Melastomataceae (Venkatesh, 1955) but the evidence involves only *Memecylon* and *Mouriri*, genera rather remote from *Rhexia* and its allies. Anthers of *Memecylon* open the "normal" way, by two complete longitudinal slits; whereas the two slits in *Mouriri* are restricted toward the apex, supposedly

⁴Pore size is one of the characters used by James (1956) to subdivide *Rhexia* into two series of species.

indicating an evolutionary stage through which all poricidal Melastomataceae have passed. As far as we are aware, however, no one has illustrated a series of transitional forms⁵ between the paired, linear openings of *Mouriri* and the solitary, circular, centrally situated pore of *Rhexia*. One might therefore propose a somewhat different explanation: that the small, rounded pore evolved as a new structure, beginning as a functionless subapical indentation between the outer anther sacs and assuming its present importance when longitudinal dehiscence was lost. Additional comparative studies of melastomataceous anthers would be very desirable.

Geotropism in the androecium of *Rhexia* deserves comment. Open flowers are oriented with floral axis away from the vertical and toward the horizontal position. Since the emerging anthers are reflexed and the pore is located on the adaxial side, the apical end of the lowermost anther (nearest the earth's surface) hangs downward with its pore directed outward. All of the other anthers are brought into positions approximately parallel to this one by a counterclockwise (as viewed from outside) twisting of the filaments, the filament farthest from the earth twisting 180°. It is interesting that in *Monochaetum*, a genus placed next to *Rhexia* in Cogniaux's (1891) monograph of Melastomataceae, the pore is located on the abaxial side of the anther. Nevertheless, the outward orientation of all pores becomes the same as in *Rhexia*, because in *Monochaetum* the lower stamens twist and the uppermost stamen does not (Troll, 1922; Ziegler, 1925). According to Ziegler, the upper filaments of *Tibouchina* twist like those of our *Rhexia* flowers. The result is the same in the three genera: all pores open toward insect visitors.

Leggett (1881) reported that the lower part of the *Rhexia* anther acts as a bellows, causing puffs of pollen to

⁵Dr. Wurdack suggests *Miconia* as a genus to examine for such transitional forms, but he adds that an adequate range of fluid-preserved material would be hard to obtain.

emerge forcefully from the pore when pressed by a bumblebee's "foot" or a pointed object in a botanist's hand. We have verified this in company with Dr. Wurdack, using a dissecting needle to apply the pressure and observing the resulting puff of pollen through a stereomicroscope. Dr. Wurdack suggests that in nature the pollen gathering behavior of the bee may be more complex than this simple observation would indicate, for he has noticed an unusually vigorous buzzing of bumblebees while they are visiting his *Rhexia* plantings. Vibrations by bee visitors are known to play a role in the floral biology of *Melastoma malabathricum* (Pijl, 1954) and of some other plants in which anthers have apical pores (Michener, 1962). The older literature describes additional complexities in the behavior of insects visiting Melastomataceae (for review, see Harris, 1905, p. 229). Accordingly, the floral biology of *Rhexia* might well be worth the attention of an enterprising graduate student with a flair for cinematography.

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